

# A new species and the phylogeny of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini)

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#### ABSTRACT

Gromphas jardim Cupello & Vaz-de-Mello sp. nov. is described from Bolivia and Central Brazil and is endemic to the biogeographic province of Rondônia. It resembles Gromphas amazonica and Gromphas inermis, but is distinguished primarily by the pattern of pronotal granulation and the form of the apical tubercle of male protibiae, which is modified in a tapered spur. Based on 31 morphological characters, a phylogenetic analysis returned a single most parsimonious tree where Gromphas is monophyletic and has the following internal topology: ((G. aeruginosa + G. lemoinei) (G. dichroa (G. inermis (G. amazonica + G. jardim)))).

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# Introduction

The South American dung beetle genus *Gromphas* Brullé, 1837 was the focus of a recent taxonomic revision presented by us (Cupello and Vaz-de-Mello 2013, 2014). In those works, we recognized *Gromphas* as a member of the subtribe Gromphadina of Phanaeini along with *Oruscatus* Bates, 1870 and composed by five species: *Gromphas lemoinei* Waterhouse, 1891, from the Llanos of Venezuela and Colombia, *Gromphas aeruginosa* (Perty, 1830) and *Gromphas amazonica* Bates, 1870, from the Amazon, *Gromphas inermis* Harold, 1869, from the Atlantic Forest and open environments (Cerrado, Chaco and Pampa) of the Southern Cone, and *Gromphas dichroa* Blanchard, 1846, from the Chaco and Pampa. All these species were redescribed and illustrated, and their taxonomy and nomenclature problems were discussed.

Yet an important question remained open regarding a specimen collected in the municipality of Cáceres, in the Alto Pantanal region of the state of Mato Grosso, central Brazil, and identified by us as a female of *G. amazonica* in Cupello and Vaz-de-Mello (2013, p. 463). On that occasion, we stated that Cáceres was an unexpected location for that species and distant more than 1000 km from the second southernmost point known for *G. amazonica*, Contamana, Peru. We also pointed out that, despite sharing several unique characteristics with the other examined specimens of *G. amazonica* (as, for example, the distinctly carinulate

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elytral striae and the apical protarsomere with a long spiniform projection), that female was different by having 'a strong green color with metallic reflections covering the entire body, especially the head and pronotum'. Having only one single specimen in hand, we judged that we did not have enough evidence to describe a new taxon and therefore it would be more prudent to consider that curious coloration as an individual variation within *G. amazonica*.

Since then, we had the opportunity to carefully examine in person two major British collections, the Hope Entomological Collection, Oxford University Museum of Natural History, Oxford, and The Natural History Museum, London, and there, mingled among specimens of *G. inermis*, we found four individuals from Bolivia (two males and two females) consistent with our Brazilian female and that finally gave us sufficient evidence to recognize the new species described herein, *Gromphas jardim* sp. nov. After presenting this sixth species of *Gromphas* and based on the morphological characteristics described here and in the previous revision (Cupello and Vaz-de-Mello 2013), we perform for the first time a phylogenetic analysis of the genus to understand the evolutionary relationships of its species and the evolution of their characters.

# **Material and methods**

Specimens cited in this work are deposited in the following collections (curators or contacts in parenthesis):

- CEMT Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Vaz-de-Mello);
- CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier);
- BMNH The Natural History Museum, London, UK (Max Barclay and Malcolm Kerley);
- MACN Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (Juan José Martínez);
- MLPA Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina (Nora Cabrera);
- MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel A. Monné and Marcela L. Monné);
- OUMNH Hope Entomological Collection, Oxford University Museum of Natural History, Oxford, UK (Darren Mann).

Descriptions, terminology, geographical distribution, measurements and citation of material examined follow the same pattern as Cupello and Vaz-de-Mello (2013) to permit easy comparison with the information published there. For measurements, in particular, the only difference is that, because the type series of *G. jardim* is restricted to just five specimens, we do not give here values of standard deviation and do not present the values for each sex separately. As in Cupello and Vaz-de-Mello (2013), the abbreviations are: TL (total length), PL (partial length), PW (greatest width of pronotum), AV (average), MX (maximum) and MN (minimum). For geographical distribution, we follow now Morrone's (2014) classification of the Neotropical region, an updated version of those schemes (Morrone 2001, 2006) cited by us in Cupello and Vaz-de-Mello (2013). To avoid redundancy, structures illustrated in Cupello and Vaz-de-Mello (2013) are not illustrated here again and the figures present in that work are cited here with lowercase letters and brackets (i.e. {fig.}).

# **Taxonomic treatment**

# Key to the species of Gromphas (modified from Cupello and Vaz-de-Mello 2013)

- Pronotum granulated and with mid-longitudinal line of smooth and glossy tegument at centre (clearly seen in {fig. 3}). Pronotal prominence formed by a pair of horizontal projections preceded by a pair of smooth concavities ({figs 1-4, 7-9}); in very small specimens, pronotal prominence absent and concavities reduced to two impressions in anterior margin of pronotum ({figs 5, 10}). Protibial spur only slightly curved apically ({figs 22, 46}). Genae and frons with smooth tegument adjacent to eyes; remaining tegument of genae and frons with squamose granulation ({figs 24, 25}).
  Pronotum smooth or with feeble granulation at centre ({figs 13, 14}); or, if granulation dense, mid-longitudinal line absent or very faint ({fig. 15}). Pronotal prominence and concavities absent. Protibial spur strongly expanded apically ({figs 21, 23, 45}). Genae and frons with strong granulation adjacent to eyes ({figs 26-28}).
- 3(1). Pygidium having basal margin ({fig. 35}). Apical meso- and metatarsomeres strongly curved ({fig. 47}). Metatibiae very thin ({fig. 42}). Posterior pronotal fossae always present. Anteromedian angle of metasternum strongly projecting, narrow and truncate apically ({fig. 49}); region in front of anteromedian angle glabrous ({figs 19, 49}). Clypeus truncate apically and not lobed ({fig. 26}), never upturned. Cephalic projection truncate apically ({fig. 33}). Colour variable, either entirely metallic green, or with blue elytra and red and blue or yellowish pronotum ({fig. 14}). Brazil (Rio Grande do Sul), Paraguay, Argentina and Uruguay (Chacoan subregion: Chacoan dominion).
  - Gromphas dichroa Blanchard, 1846 Pygidium lacking basal margin ({fig. 36}). Apical meso- and metatarsomeres only slightly curved apically ({fig. 48}). Metatibiae very broad and robust ({fig. 41}). Posterior pronotal fossae usually absent ({fig. 43}); if present, then subtle and touching posterior margin of pronotum (Figures 1E and 4). Anteromedian angle of metasternum wide and rounded apically, not projected ({figs 50–51}); region in front of the anteromedian angle with evident pilosity ({figs 18, 20, 50, 51}). Clypeus with four lobes ({figs 27, 28}) and folded upward. Cephalic projection emarginate apically ({figs 32, 33}) (in very small and worn specimens, apex rounded or truncate).
- 4(3). Elytral striae simple. Pronotum with strong granulation in centre, only posterior region completely smooth ({figs 15, 43}). Posterior margin of pronotum projecting at middle ({fig. 15}). Metatibial spur straight apically ({fig. 40}). Apical tubercle of male protibia tiny and almost imperceptible ({fig. 23a,b}). Apical protarsomere (present only in females) short, without spiniform prolongation ({fig. 46}). Colour variable, either black, green, copper, or a combination of those

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5 (4) Apical tubercle of male protibia prolonged as a long non-articulated spur with a row of setae in its dorsal surface ({fig. 21b; arrow}). Ventral carina of protibia with a row of tubercles in males ({figs 20d, 23b}) and simple in females ({fig. 23a}). Pronotal granulation, in lateral view, not reaching posterior margin of pronotum (Figure 3B). Cephalic projection very wide, and, in major specimens, with apex of equivalent width of distance between apices of apical lobes of clypeus ({fig. 27}). Colour black, dark blue, or reddish-brown without metallic reflections. Colombia, Brazil and Peru (Brazilian subregion: Boreal Brazilian and South Brazilian dominions)...... Gromphas amazonica Bates, 1870 Apical tubercle of male protibia modified in a short and tapered spur lacking any row of setae in its dorsal surface; apical tuft of setae independent of this spur (Figure 2A,B). Ventral carina of protibia simple in both sexes (Figure 2A). Pronotal granulation, in lateral view, reaching posterior margin of pronotum (Figure 3A). Cephalic projection narrow, with apex much narrower than distance between apices of apical lobes of clypeus (Figure 1F). Colour dark olive green and copper with metallic reflections. Bolivia and Central Brazil (Brazilian subregion: South Brazilian dominion)...... Gromphas jardim sp. nov.

# **Gromphas jardim** Cupello and Vaz-de-Mello sp. nov. (Figures 1–7)

*Gromphas lacordairei*: Hamel-Leigue et al., 2006: 6, fig. 49,50; Hamel-Leigue et al., 2009: 61 (part), 49 (part), fig. 14 (part), figs 27,28.

Gromphas amazonica: Cupello and Vaz-de-Mello 2013: 463 (all the fifth paragraph of 'Intraspecific variation and taxonomic discussion' section).

### Type specimens

Holotype: **BOLÍVIA**: BENI: Moxos, Río Ichiguita, 155 m, 15°08'S, 65°18'W, 20.V.2005, C. Hamel and T. Vidaurre cols. – male (OUMNH) ["BOLIVIA: Beni, Rio Ichiguita, 155 m., 15°08' S 65°18'O, 20.v.2005, Sabana. Trap. cebo heces humano. prep./col.: C. Hamel, T. Vidaurre", "Gromphas lacordairei Brullé, 1834 det. A. C. Hamel. OUMNH-2006-097", "Trap 7", "HOLOTIPO", "HOLOTYPE. Gromphas jardim sp. nov. Cupello & Vaz-de-Mello des. 2014 d"] (Figure 1A–D, F). Aedeagus extracted and genital capsule glued in a triangular label and internal sac placed in a microvial with glycerine, all pinned with the holotype.



**Figure 1.** *Gromphas jardim* sp. nov. (A–D) Holotype. (A) Dorsal view. (B) Lateral view. (C) Aedeagus. From left to right, dorsal, lateral and ventral views. (D) Labels. (E) Female paratype from Bolivia. (F) Dorsal view of head (holotype). (G) Frontal view of cephalic projection (male paratype).



**Figure 2.** Protibia of *Gromphas jardim* sp. nov. (A, B) Male protibia: (A) Ventral view, (B) Dorsal view. Red arrow indicates apical tubercle modified in a tapered spur. (C) Female protibia. Note that the apical tuft of setae is much denser and longer in male than in female.



**Figure 3.** Lateral view of pronotum. (A) *Gromphas jardim* sp. nov. (B) *Gromphas amazonica*. Note that the granulation extends much more posteriorly in *G. jardim*, reaching the pronotal posterior margin, than in *G. amazonica*, wherein the granulation is absent or rudimentary in posterolateral region after lateral fossa.



**Figure 4.** Male paratype of *Gromphas jardim* sp. nov. and its labels (braces '{' joining two sides of a same label). We believe that the French zoologist and explorer Alcide d'Orbigny was the collector of this specimen in 1832 (see the text).

Paratypes: **BRAZIL**: MATO GROSSO: Cáceres, 10 October 2008, E. Silva col. – 1 female (CEMT; specimen identified in Cupello and Vaz-de-Mello (2013, pp. 463–464) as *G. amazonica*). **BOLÍVIA**: BENI: Moxos, Río Ichiguita, 155 m, 15°08'S, 65°18'W, 19 May 2005, C. Hamel and T. Vidaurre cols. – 1 female (MNRJ) and 1 female (OUMNH). COCHABAMBA: Territory of the Yuracaré people ("Juacares Indians"), north side of the Cordillera de Cochabamba ("Cortillera de Cochabamba"), without date and collector (probably collected by Alcide d'Orbigny in 1832; see comments below) – 1 male (BMNH).

# Etymology

The specific name, a noun in apposition, is a patronym honouring Arlindo da Silva Jardim (1923–2014), Brazilian aviator and grandfather of the first author. Having grown up in the small, rural village of Dom Viçoso, Minas Gerais, Arlindo Jardim achieved his childhood dream and flew professionally worldwide for over four decades. He will remain as a source of inspiration for MC.

### Description

*Colour.* Anterior region of clypeus black; remainder of head and pronotum with dark olive green and copper metallic reflections. Elytra, metasternum, ventral surface of legs and pygidium dark olive green with metallic sheen and silky appearance. Ventrites entirely black or black with week metallic green reflections.

*Head.* Margin of clypeus with four lobes (Figure 1F) and distinctly upturned. Genae and frons completely granulate, including region adjacent to eyes (Figure 1F). Cephalic projection a raised carina with converging sides and emarginate apex in major specimens (Figure 1G); apex narrower than distance between apices of apical lobes of clypeus (Figure 1F).

*Thorax.* Pronotum convex; lateral region with dense granulation reaching the posterior margin (Figure 3A), density of granulation decreasing posteromedially; posteromedian region smooth or with strongly effaced granulation (Figures 1A, E, 4); posterior fossae apparent only as two very shallow and sometimes only weakly indicated impressions removed from the pronotal posterior margin (Figures 1E, 4). Posterior margin of pronotum rounded.

Mesosternum with dense pilosity. Metasternum with fine and sparse punctation at centre. Anteromedian angle of metasternum convex and with globose apex; area in front of anteromedian angle with evident setae.

*Legs.* Protibia slightly narrower in males than in females (Figure 2); in ventral view, longitudinal carina simple in both sexes (Figure 2A). Space between protibial lateral teeth deeper in males than in females (Figure 2). Protibial spur with apex strongly expanded and curved downward (Figure 2). Inner apical angle of protibia with a tuft of setae longer and denser in males than in females; in males, tubercle of inner apical angle developed as a short and tapered spur independent of apical tuft of setae (Figure 2). Apical protarsomere with a long, distal spiniform prolongation. Mesotarsi and metatarsi with apical tarsomere slightly curved at apex. Metatibia very broad and robust. Metatibial spur with apex distinctly curved.

*Elytra.* Striae very fine and, especially striae 1–4, carinulate from base to half or apical two-thirds of elytra. Sutural margin glossy and only sparsely punctate; basal half of sutural margin with sheen extending laterally onto first or second interstria.

*Abdomen.* Pygidium lacking basal margin and with irregular sculpture. Groove of propygidium extending to base of pygidium. Abdominal sternites microsculptured and sparsely punctuated.

*Aedeagus.* Apex of phallobase, in ventral view, with membranous area expanded triangularly in the middle (Figure 1C). Medial sclerite only slightly curved, almost flat.

#### Measurements (four specimens: two males and two females)

TL: AV: 15.2; MX: 16.3; MN: 13.9. PL: AV: 12.3; MX: 13; MN: 11.7. PW: AV: 8.5; MX: 9; MN: 8.

### Intraspecific variation and taxonomic discussion

At a first glance, *G. jardim* resembles superficially *G. amazonica* and, to a lesser degree, *G. inermis*, and, in fact, has been confused with these species both in collections and recent publications. Deposited at the BMNH, the oldest specimen known to us bears four labels with different identifications (Figure 4): an older, which by the calligraphy we assign to Charles O. Waterhouse, former curator of entomology at the BMNH, has written 'Gormphas amazonicus Bates', while the other two more modern labels identify that specimen, respectively, as *G. amazonica* and 'G. lacordairei Brullé, 1834', an unavailable name referring to *G. lacordairei* 

Burmeister, 1874, junior synonym of G. inermis (see more in Cupello and Vaz-de-Mello 2013). The fourth label has handwritten the word 'Coproides', but the remaining information is effaced and completely unreadable. d'Olsoufieff (1924) examined a specimen of G. amazonica in the Muséum national d'Histoire naturelle, Paris, labelled 'coproides Dej. Cayenne (coll. Mniszech)' and probably the unavailable name 'coproides' was used before the description of G. amazonica by Bates (1870) as a name in litteris to refer to this species. The three specimens found in OUMNH, in turn, including the holotype, are part of a large series of dung beetles recently collected in Bolivia and the basis for the works of Hamel-Leigue et al. (2006, 2009); they were identified and illustrated in these publications as 'G. lacordairei Brullé'. The geographical distribution and probably the other information present for 'G. lacordairei Brullé' in Hamel-Leigue et al. (2006, 2009) have mixed data belonging in fact to G. jardim and G. inermis. Similarly, as said in the Introduction of the present work, in Cupello and Vaz-de-Mello (2013), we provisionally identified the specimen (now paratype) from Cáceres as a G. amazonica. Now, in possession of a greater number of specimens, the differences between G. jardim, G. inermis and G. amazonica became much clearer.

Gromphas jardim shares only with G. amazonica, G. inermis and G. dichroa the characters: genae and frons granulated adjacent to eyes (Figure 1F), absence of pronotal prominence, protibiae narrower in males than in females (Figure 2), and protibial spur expanded at apex (Figure 2); only with G. amazonica and G. inermis, G. jardim shares the character margin of clypeus with four lobes (Figure 1F). Probably this last characteristic, which is an apomorphy shared by them (see the phylogenetic analysis below), was the main cause for the past misidentifications.

Yet *G. jardim* is easily differentiated from *G. inermis* by having metatibial spur distinctly curved apically (straight in *G. inermis*), posterior margin of pronotum rounded (projected at middle in *G. inermis*), elytral striae carinulate (simple in *G. inermis*), and metasternum and sutural margin of elytra with fine and sparse punctation (dense punctation in *G. inermis*); furthermore, pronotal hump and sutural margin of elytra raised are present in major specimens of *G. inermis* but absent in *G. jardim* (Figure 1B). On the other hand, the medial sclerite of the internal sac of *G. jardim* is very similar to that of *G. inermis* and no significant difference between them was found ({fig. 59}).

From *G. amazonica*, *G. jardim* is differentiated most easily by the shape of the apical tubercle of male protibia, which, although much more developed in *G. jardim* than the tiny and almost imperceptible tubercle of the other four species of *Gromphas*, is still much smaller than that of *G. amazonica*; in *G. jardim*, the tubercle has the shape of a tapered spur and is separated from the apical tuft of setae, which rests adjacent to the spur (Figure 2A,B); in *G. amazonica*, the spur is long, laterally flattened and curved and has the tuft of setae on its dorsal surface as a row of setae. The shape of the cephalic projection of *G. jardim* is similar to that of *G. inermis*, i.e. it is narrower than the distance between the apices of the apical lobes of clypeus (Figure 1F), while that of *G. jardim* and *G. amazonica* are: the colour, which is dark olive green and has metallic reflections in *G. jardim*, but black, dark blue, dark green or reddish-brown and never has metallic reflections

in *G. amazonica*; and the pronotal granulation, which penetrates more the posterior portion of the pronotum and, in lateral view, reaches the posterior margin in *G. jardim* (Figure 3A), whereas in *G. amazonica* the granulation is restricted to the anterior portion of the pronotum and never reaches the posterior margin (Figure 3B). The form of the granules of the head and pronotum is also distinct between the two species, being wider and flattened in *G. amazonica* and more rounded and smaller in *G. jardim* (this second form is very similar to that of *G. inermis*). Finally, the longitudinal carina of the ventral surface of protibia is simple in both sexes of *G. jardim*, resembling *G. aeruginosa* and *G. lemoinei*, but is distinct to that of *G. amazonica*, *G. inermis* and *G. dichroa*, which, in males, has a row of tubercles on its basal half and, in females, is simple. The constant presence of the posterior pronotal fossae in *G. jardim* also distinguishes this species from *G. inermis* and *G. amazonica*, in which these fossae are usually absent.

The spiniform projection at the apex of apical protarsomere was not observed in one of the three females of *G. jardim* examined by us, and we believe that this is due to the wear, as happens in some *G. amazonica*, the only other species of *Gromphas* that has this kind of apical protarsomere (Cupello and Vaz-de-Mello 2013). On the other hand, the nature of the posterior pronotal fossae varies: in the two males observed, the fossae are clearly marked and easily visible to the naked eye, whereas those of the three females are much less marked and almost imperceptible. Whether this is a case of individual or sexual variation is difficult to say until the examination of a larger number of specimens of both sexes.

#### Geographic distribution

Brazilian subregion: South Brazilian dominion: Rondônia province. **BRAZIL**: MATO GROSSO: Cáceres. **BOLÍVIA**: BENI: Moxos. COCHABAMBA: 'Territory of the Yuracaré people, north side of the Cordillera de Cochabamba' (Figure 5).

#### Comments

While the holotype and the three female paratypes of G. jardim were collected in the 21st century and have label information detailed enough to permit an easy understanding of their origin, the male paratype is much older and has a puzzling history. Only one of the five labels attached to this specimen before our work has information about its provenance (Figure 4). This label is circular and has 'Bolivia' written on one side and '46/76', on the other side. According to Max Barclay (pers. comm.), '1846–76 refers to a collection, all with the same data, acquired in 1846 and including 325 Coleoptera and 250 Lepidoptera', and these collecting data are 'Territory of Juacares Indians (north side of the Cortillera (sic) de Cochabamba)'. We believe that 'Juacares Indians' refers to the Yuracaré, an indigenous people resident on the north side of the Cordillera de Cochabamba, in the department of Cochabamba, Bolivia. To our knowledge, the only European naturalist who crossed this remote region before 1846 was the French zoologist and explorer Alcide d'Orbigny (1802–1857), who visited a Yuracaré village on May 28 1832 and stayed there for 4 days (Papavero 1971). Indeed, d'Orbigny described and illustrated in detail this people in his great work Voyage dans l'Amérique Méridionale (d'Orbigny 1835-1847). So we believe he was the probable collector of the male paratype of G. jardim. This finding is also



Figure 5. Updated distribution of the six species of Gromphas.

interesting because, if correct, it indicates that not all insects collected by Alcide d'Orbigny are deposited in the Muséum National d'Histoire Naturelle, Paris, France, as suggested by Horn and Kahle (1936) and Evenhuis (1997).

# **Bionomics**

The label data indicate that the holotype and the two paratypes from Beni, Bolivia, were collected in traps baited with human faeces in open habitats. These specimens also had some unidentified phoretic mites attached to their legs, especially to the metatarsi. The recorded months for *G. jardim* are May and October.

# Gromphas aeruginosa (Perty, 1830) (Figures 5, 6)

#### New geographical records

**Brazil**: Rondônia: Guajará-Mirim. **Peru**: Loreto: Alto Amazonas (Yurimaguas), Mariscal Ramón Castilla (Pebas). Madri de Dios: Tambopata National Reserve. **Bolivia**: Beni: José Ballivián (Rurrenabaque), Mamoré (San Ramón). Cochabamba: Carrasco (Valle de Sacta).

# Additional material examined

**BOLIVIA:** no more data – 1 male and females (BMNH) and 1 male (OUMNH – Hope-Westwood coll.). BENI: José Ballivián, Rurrenabague, Río Beni, XII (without year), W. M. Mann col. – 1 female (BMNH); Mamoré, San Ramón, Estancia San Lorenzo, 13°26'55"S, 64° 36'15"W, 1 December 2003, D. J. Mann and C. Hamel cols. – 1 female (OUMNH). COCHABAMBA: Carrasco, Valle de Sacta, 17°06'S, 64°47'01"W, 09.V.2000, A. C. Hamel col. – 1 male and 1 female (OUMNH). SANTA CRUZ: Ichilo, Buena Vista, 1922, R. C. Robert col. – 1 male (BMNH); same location, October 1922, J. Steinbach col. – 2 males (BMNH); Sara, November to December1922, J. Steinbach col. - 1 female (BMNH). BRAZIL: Amazon, without date, H. W. Bates col. - 2 males and 1 female (BMNH); Rio Madeira, without year and collector – 4 males (BMNH). AMAZONAS: Tefé ('Ega'), without date and collector (H. W. Bates col.?) - 4 males and 1 female (BMNH); Tefé ('Ega'), January to April1879, M. de Mathan col. - 2 males (BMNH). PARÁ: without date, A. Miles Noss col. – 1 male and 1 female (BMNH). RONDÔNIA: Guajará-Mirim (?; 'Lake Mirim, Guayara'), 8 June 1937, P. Bullivian col. - 1 male and 1 female (BMNH). PERU: Loreto: Alto Amazonas, Yurimaguas ('Jurimaguas'), without date and collector - 1 female (BMNH); Mariscal Ramón Castilla (Pebas), without date and collector - 2 males and 2 females (BMNH). Madre de Dios: Tambopata National Reserve, 30 km (air) southwest Puerto Maldonado, 280 m, 12°50'S, 06°20'W, 5 March 1982, N. E. Stork col. – 1 female (BMNH). Ambiguous data: (Villa Nova (country?), no more data – 1 female (BMNH). No data: 3 males (MACN - Hermann Burmeister coll.).

# Gromphas lemoinei Waterhouse, 1891 (Figures 5–6)

#### Additional material examined

VENEZUELA: TÁCHIRA: Santo Domingo, Sta. Rosa Valz, 13 August 1983, Havranek (?) col. – 1 male (BMNH).

# **Gromphas dichroa** Blanchard, 1846 (Figures 5, 6)

#### **Comments**

Although only nine specimens of G. dichroa were examined in Cupello and Vaz-de-Mello (2013), we recognized a wide colour variation in this species. Now, having examined the MACN collection, we found other seven specimens collected between 1926 and 1927 in

Santo Tomé, Corrientes, Argentina, a locality already recorded for this species. This series is very interesting because it shows for just one locality much of the colour variation described by us earlier, including specimens that are entirely green, with green pronotum and dark blue elytra, and with pronotum metallic green on sides and along posterior margin and greenish-red in centre and dark blue elytra. This finding supports our hypothesis that colour varies individually within at least some populations, and it is not necessarily a matter of geographic variation nor evidence for recognizing more than one taxa. Yet, as pointed out by one of the anonymous reviewers of this work, 'the fact that the colour is subject to wide variation in one of the studied populations does not implicate that this variation necessarily occurs in the other populations of this species. There is the probability that some populations bear just a single or two colours'. We agree that this is a possible scenario and so more collecting is needed for a fuller understanding of colour variation in *G. dichroa*.

The female from the Hermann Burmeister collection has one of its tarsi complete (i.e. it is not broken as in all the other females examined) and it is identical to the tarsus of *G. inermis*: the apical protarsomere is short and lacks an apical spiniform prolongation.

# Additional material examined

**ARGENTINA**: CORRIENTES: Santo Tomé, September 1926, without collector – 1 male (MACN); Santo Tomé, February 1927, without collector – 2 males and 2 females (MACN); Santo Tomé, October 1928, without collector – 1 male (MACN). **URUGUAY**: December 1894, without collector – 1 female (MACN – Hermann Burmeister coll.). SALTO (?): without date, Hermano Mario col. – 1 male (MLPA). MONTEVIDEO: without date, J. Tremoleras col. – 1 male (MLPA).

# Gromphas inermis Harold, 1869 (Figures 5, 6, 8A)

#### New geographical records

**BOLIVIA**: Tarija: Gran Chaco (Yacuiba). **PARAGUAY**: Paraguarí: Sapucaí. **ARGENTINA**: Jujuy. Tucumán. Córdoba: Leones. Santa Fe: General Obligado (Villa Ana), Rosario, Santa Fe. Misiones: San Ignacio, Puerto Iguazú. Corrientes: San Roque. Entre Ríos: Villa Paranacito. Buenos Aires: Isla Martín García, Pergamino, San Pedro. Mendoza. **URUGUAY**: Colonia: Riachuelo. Canelones: Atlántida.

#### Comments

In Cupello and Vaz-de-Mello (2013), we cited the occurrence of *G. inermis* in the Bolivian department of Beni based on the report of this species (cited as '*G. lacordairei* Brullé') by Hamel-Leigue et al. (2009). Nonetheless, we know now that the specimens examined by them from Beni are, in fact, *G. jardim*, and so Beni and the biogeographic province of Rondônia (former Pantanal province, as cited in Cupello and Vaz-de-Mello 2013) should be disregarded as an area of occurrence of *G. inermis*. On the other hand, localities of the Chacoan province in the departments of Tarija and Santa Cruz, also cited by Hamel-Leigue et al. (2009), are indeed places where *G. inermis* is present. The occurrence of this

species in the Argentine province of Mendoza, as first reported here, is the most western record known for *G. inermis* (Figure 5).

During our examination of specimens for the revision of *Gromphas*, we found a female from Artigas, Uruguay, that is very interesting by being matte black and having the pronotal surface completely irregular; nonetheless, taking into account all the other characteristics, it fits in *G. inermis*, and so we identified that specimen with this name in Cupello and Vaz-de-Mello (2013). Since then, we examined the Hermann Burmeister collection, housed in MACN, and there we found two other Uruguayan females (from 'Banda Orient.') with a very similar colour and irregular pronotum that were identified by Burmeister with the unavailable name '*Gromphas rugicollis* Nob.'. For now, we consider these differences as intraspecific variations of *G. inermis* (possibly teratological specimens); we observed black specimens of *G. inermis* from other regions and, in fact, black and brown colorations seems to be related to teneral specimens, which would also explain the irregular surface of pronotum. All the other Uruguayan specimens examined by us are typical *G. inermis*.

## Additional material examined

ARGENTINA: 1904, O. W. Thomas col. - 1 male and 1 female (BMNH); Río Bermejo, without date, H. Richter col. - 1 male and 1 female (MLPA); Río Salado, no more data - 2 males and 2 females (BMNH). BUENOS AIRES: no more data - 2 males (BMNH), 1 female (MACN); without date, H. Richter col. - 2 males and 3 females (MLPA); without date, J. Bosq col. – 1 male and 1 female (MLPA); October 1898, C. Bruch col. - 1 female (MLPA); 10 September 1903, Carlos Bruch col. - 1 male (MACN – Carlos Bruch coll.); 2 March 1904, A. Zotta col. – 1 male (MACN); without locality, Deceber 1921, without collector - 1 male and 1 female (MACN); without locality and date, J. Boso col. - 1 male and 1 female (MACN); 17 km south of Buenos Aires, 8 January 1980, C. and M. Vardy cols. - 1 female (BMNH); Isla Martín Garcia, April 1937, M. J. Viana col. - 1 male (MACN); La Plata, no more data - 2 males (BMNH) and 1 male (MACN); La Plata, without date, A. R. Bezzi col. – 1 male and 1 female (MLPA); Pergamino, February 1949, without collector – 1 male (MLPA); San Isidro, Martínez, 16 February 1924, M. Sires col. – 1 female (MACN); San Pedro, without date, A. G. Frears - 1 male (MACN). CHACO: no more data - 2 males and 1 female (MACN); December 1895, Carlos Bruch col. – 1 male (MACN – Carlos Bruch coll.). CÓRDOBA: no more data – 1 male (BMNH); without date, H. Richter col. – 1 male and 1 female (MLPA); Leones, 30 January 1946, W.N.P. col. – 1 female (MACN). CORRIENTES: no more data – 1 male and 2 females (MACN), 1 male (MACN – Carlos Bruch coll.), and 2 males and 5 females (MLPA); San Roque, February 1920, Bosq col. - 1 male (MLPA); Santo Tomé, no more data - 4 males and 6 females (MACN); Santo Tomé, October 1925, without collector – 4 males and 1 female (MACN); Santo Tomé, September 1926, without collector – 1 male (MACN). ENTRE RIOS: no more data – H. Richter col. – 1 male and 1 female (MLPA); Villa Paranacito, no more data – 1 male (MACN). JUJUY: no more data – 1 male and 1 female (MACN) and 2 males and 1 female (MLPA). MENDOZA: no more data – 1 male and 2 females (BMNH). MISIONES: no more data – 8 males and 3 females (MACN); without date, illegible collector – 1 female (MLPA); without date, C. Bruch col. – 1 female (MLPA); without date, H. Richter col. – 1 male and 1 female (MLPA); Alto Paraná, 1–18 December 1933, K. J. Hayward

col. – 1 female (BMNH); San Ignacio, 1928–1929, Quiroga col. – 2 males (MACN); San Ignacio, 21 October 1929, without collector – 1 male (MLPA); Puerto Iguazu, October 1927, without collector – 1 female (MACN). SALTA: without date, H. Richter col. – 1 male (MLPA). SANTA FÉ: Chaco, without date, H. Richter col. – 7 males and 4 females (MLPA); Estancia La Noria, Rio San Javier, 8–20 December 1911, G. E. Bryant col. – 8 males and 9 females (BMNH); General Obligado, Villa Ana, FCSF, November 1924, K. J. Hayward col. - 1 male (BMNH); Rosario, without date, A. Stévenin col. - 1 male (MACN); Santa Fé, no more data – 1 male (MLPA). SANTIAGO DEL ESTERO: Río Salado, without date, Wagner col. – 2 females (MLPA). TUCUMÁN: no more data – 1 male and 1 female (BMNH); without date, H. Richter col. – 3 males and 3 females (MLPA). BOLÍVIA: SANTA CRUZ: Chiquitos, Santiago, 18°20'17"S, 59°35'37"W, November 1959, without collector – 1 male (CMNC; examined by photo). TARIJA: Gran Chaco, between Yaguacua-Caiza, 21°50'52"S, 63°36'26"W, 620 m, 3 January 2005, Mann, Hamel and Herzog cols. – 3 males and 1 female (BMNH) and 35 males and 43 females (OUMNH); Gran Chaco, Yacuiba, 622 m, 21°54′03″S, 63°37′54″W, 3 January 2005, Mann, Hamel and Herzog cols. – 1 female (BMNH). BRAZIL: no more data – 1 female (OUMNH - Hope-Westwood coll.). MATO GROSSO: without date, Koslomosky (?) col. – 3 males (MLPA); Poconé, Rodovia Transpantaneira, 8 February 2015, Mario Cupello col. – 1 male (MNRJ). MATO GROSSO DO SUL: Corumbá, Alto Paraguai, without date, H. Richter col. - 1 male (MLPA). RIO GRANDE DO SUL: no more data - 4 males and 1 female (BMNH); 7 November 1959, C. Biezanko col. - 1 female (BMNH); 20 October 1961, C. Biezanko col. – 1 male (BMNH); January 1995, M. A. Fernando (?) col. – 1 male (MACN); Pelotas, 10 November 1953, C. M. Biezanko col. – 1 female (BMNH). SANTA CATARINA: no more data – 3 females (BMNH); March 1820 – 1 female (OUMNH – Hope-Westwood coll.). PARAGUAY: no more data – 1 male (BMNH) and 1 male (MACN); without date, H. Richter col. - 1 male (MLPA); 1908, F. O. Lucas col. - 1 male and 1 female (MLPA). DISTRITO CAPITAL: Asunción, September 1922 to April 1923, E. G. Kent col. – 1 female (BMNH). GUAIRÁ: Villarrica, without date, H. Richter col. – 1 male and 2 females (MLPA). PARAGUARÍ: Sapucai, 1903, W. Foster col. – 2 females (BMNH). URUGUAY: no more data - 2 females (BMNH), 2 males and 2 females (MACN – Hermann Burmeister coll.). CANELONES: Atlántida, no more data – 1 male (MACN). COLONIA: no more data – 1 male (MACN); Riachuelo, without date, A. Stévenin col. – 1 male (MACN). MONTEVIDEO: no more data – 1 male (BMNH); Carrasco, no more data – 1 female (MACN); Peñarol, 20 December 1929, without collector – 1 female (MLPA); Peñarol, 10 October 1933, without collector – 1 female (MLPA). Ambiguous data: 'Fives Lille, Bruch-Waiser' - 2 males (MACN - Carlos Bruch coll.); 'Parana. Nov.' (Argentina or Brazil?) – 1 male (MACN – Hermann Burmeister coll.). Specimens surely mislabeled: COLOMBIA: no more data - 1 female (BMNH – Frey coll.). No data: 1 male (MACN – Carlos Bruch coll.), 1 male and 1 female (MACN – Hermann Burmeister coll.), 1 male and 4 females (OUMNH – Hope-Westwood coll.), and 1 female (OUMNH – Gory coll.).

### **Phylogenetic analysis**

The phylogenetic analysis performed here had three main goals: to test the monophyly of *Gromphas*, to know the phylogenetic relationship of its species, and, therewith, to raise hypotheses about the transformation of their characters through the evolutionary process. In recent works (Philips et al. 2004; Cupello and Vaz-de-Mello 2013), it was well demonstrated that Gromphas is a member of the tribe Phanaeini and closely related to Oruscatus; together, these two genera form the monophyletic subtribe Gromphadina. The monotypic genus Bolbites Harold, 1868, previously considered to be related to this clade, was transferred to Phanaeina by us (Cupello and Vaz-de-Mello 2013) based primarily on the results of the phylogenetic analysis of Philips et al. (2004; morphological data) and of Ocampo and Hawks (2006; molecular data), besides other published information about the nesting behaviour of these three genera (e.g. Cabrera-Walsh and Gandolfo 1996; Halffter and Edmonds 1982; Sánchez and Genise 2008). In Phanaeina, Bolbites is sister of the lineage comprising the remaining genera of the subtribe (Philips et al. 2004; Ocampo and Hawks 2006). Taking these information into account, we selected as outgroups one of the two species of the undoubtedly monophyletic Oruscatus, Oruscatus davus (Erichson, 1847), and one Phanaeina, Bolbites onitoides Harold, 1868, the latter used to root the tree and selected among the Phanaeina by its close morphological similarity with Gromphadina.

Based on 31 informative morphological characters (see below and Table 1), an exhaustive search (implicit enumeration) was conducted using the program TNT (Goloboff et al. 2008) with Fitch parsimony and equally weighted characters, which resulted in a single tree (Figure 6) of length 46, consistency index 78 and retention index 77, both indices calculated in WinClada (Nixon 1999–2002). Supports of clades were calculated in TNT using both Bootstrap and decay index (Bremmer support) values, this last index based on a search of the 88 suboptimal trees with up to 10 steps longer than the optimal tree. The most parsimonious tree was edited in WinClada, where unambiguous characters were plotted. The ambiguous characters, on the other hand, were individually optimized based on scenarios considered more likely by us and discussed throughout the text below.

### **Character statements**

The character statements, i.e. the characters (including locators, variables and variable qualifiers) and their states, were presented following Sereno's (2007) proposals. As a result, 31

	Characters	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3								
Species	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Bolbites onitoides	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	_	_	0	0	0	0	0	0	0	-
Oruscatus davus	0	1	0	1	0	-	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	-	_	0	0	1	0	0	1	1	-
Gromphas	0	0	0	1	2	-	1	0	1	0	1	1	1	0	2	1	-	0	1	1	1	0	0	1	1	1	0	1	2	1	1
aeruginosa																															
Gromphas	0	0	0	1	2	-	1	0	1	0	1	1	1	0	1	1	-	0	1	1	1	0	0	1	1	0	0	1	2	1	1
lemoinei																															
Gromphas dichroa	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	2	1	0	0	1	0	0	1	0	1	1	1	0	1	3
Gromphas inermis	1	0	1	0	1	1	0	1	0	1	1	1	1	0	1	0	2	1	0	0	1	0	0	1	0	0	1	1	2	1	2
Gromphas	1	0	1	0	1	0	-	1	0	1	1	1	1	0	2	0	2	1	0	0	1	1	1	1	1	1	1	1	2	1	2
amazonica																															
Gromphas jardim	1	0	1	0	1	1	0	0	0	1	1	1	1	0	2	1	-	1	0	0	1	1	1	1	1	1	1	1	2	1	2

Table 1. Matrix used for the phylogenetic analysis.



**Figure 6.** Phylogeny of *Gromphas*. Above: Cladogram showing the phylogenetic relationship of the species of *Gromphas* and the evolution of their characters. Black circles indicate uncontroverted synapormorphies; white circles with black margin, controverted synapomorphies; red circles, ambiguous uncontroverted synapomorphies; and white circles with red margin, ambiguous controverted synapomorphies. Below: Support values given for each clade are decay index (above branch) and bootstrap (below branch).

informative morphological characters were found by us, of which 26 are binary and five multistate.

# Head

- 1. Clypeus, apical margin, form: straight or only slightly upturned (0); clearly bent upward (1).
- 2. Clypeus, apical margin, shape: with two lobes (0) (Figure 1F); truncate (1) ({fig. 26}).
- 3. Clypeus, lateral margin, shape: rounded (0) ({figs 24-26}); lobate (1) (Figure 1F).
- Genae, tegument, sculpture adjacent to eyes: granulose (0) (Figure 1F); smooth (1) ({figs 24, 25}).
- 5. Cephalic projection, shape: wide carina (0); carina with base wider than apex (1) (Figure 1G); horn flattened anteroposteriorly (2) ({figs 29,30}).
- 6. Cephalic projection, carina with base wider than apex, apex, shape: truncate (0) ({fig. 33); emarginate (1) (Figure 1G).



**Figure 7.** Metepisterna. (A) *Gromphas jardim* sp. nov.: *gromphas* is unique among the Phanaeini by not showing any trace of a metepisternal tab (MTab) covering the epipleural margin, a synapomorphy of this genus. (B) *Oruscatus davus*: Both species of *Oruscatus* have a small but evident MTab (indicated by red arrow). (C) *Bolbites onitoides*: The MTab of *Bolbites* is strongly developed and the dorsal margin of metepisternum is highly curved. This is the same form seen in the rest of Phanaeina and is a synapomorphy of this taxon. (D) *Dichotomius fissus* (Harold, 1867): MTab in a non-Phanaeini. This structure is present also in a series of other Coprini, as well as in at least some Oniticellini and Onitini.

# Thorax

- Pronotum, centre, mid-longitudinal line of smooth and glossy tegument: absent (0); present (1).
- 8. Pronotum, posterior fossae: present (0); absent (1).
- 9. Pronotum, pronotal prominence: absent (0) (Figures 1, 3, 4); present (1) ({figs 1-11}).
- Pronotum, form: irregular surface with single transverse depression or pair of depressions in its anterior region (0) ({figs 1–11}); entirely convex and without any king of depression (1) (Figure 1, 3, 4).
- 11. Mesepimeron, metepisternum and outer sides of metasternum, pilosity: with long and abundant setae (0) (Figure 7B,C); entirely glabrous (1) (Figure 1B, 7A).
- 12. Metepisternum, metepisternal tab: present (0) (Figure 7B,C); absent (1) (Figure 7A).
- Metasternum, sides of anteromedian angle, tegument, sculpture: smooth (0); granulose (1) ({figs 49–52}).
- 14. Metasternum, apex and region in front of anteromedian angle, pilosity: with evident pilosity, short or long (0); entirely glabrous (1).



**Figure 8.** Lateral view of male protibia, ornamentation of ventral carina. (A) *Gromphas inermis*: a row of tubercles (indicated by red arrow), a synapomorphy of clade B of *Gromphas*. (B) *Oruscatus davus*: a single large tooth. (C) *Bolbites onitoides*: a large central tooth with minor lateral teeth.

15. Metasternum, centre, tegument, sculpture: irregular (0); densely punctate (1); with fine and sparse punctation (2).

# Protibia

- 16. Ventral longitudinal carina: ornamented with tubercles and/or teeth in males and simple in female (0) ({figs 20d, 23b}); simple in both sexes (1) ({fig. 22}).
- 17. Ventral longitudinal carina, ornamentation, form: large tooth and small irregular teeth on the middle (0) (Figure 8C); a single large tooth (1) (Figure 8B); a row of tubercles on the basal half (2) (Figure 8A, {figs 20d, 23b}).
- 18. Protibial spur (articulated spur), apex, shape: only slightly curved (0) ({fig. 22}); strongly expanded (1) ({fig. 23}).
- 19. Apical tuft of setae, sexual dimorphism: denser and longer in males than in females (0) ({fig. 23}); with same density and length in both sexes (1) ({fig. 22}).
- 20. Overall shape, sexual dimorphism: narrower in males than in females (0) ({fig. 23}); very broad in both sexes (1) ({fig. 22}).
- 21. Inner apical angle, tubercle: absent (0); present (1) ({fig. 23b}).

- 22. Inner apical angle, tubercle, form: tiny and almost imperceptible (0) ({fig. 23b}); developed into a strong spur clearly visible to the naked eye (1) (Figure 2A,B; {fig. 21b}).
- 23. Apical protarsomere, apex: tapered and only slightly elongate at apex (0) ({figs 22, 46}); with a long spiniform projection (1) ({fig. 45}).

# Elytra

- 24. Elytral striae, basal fossae: present (0); absent (1).
- 25. Elytral striae, sculpture: very fine and simple, not carinulate (0); especially those more internal, carinulate from base to at least mid-length of elytra (1) ({figs 37, 38}).
- 26. Sutural margin, tegument, sculpture: densely punctate (0); with fine and sparse punctation (1).
- Sutural margin, tegument: sheen and punctation limited to sutural margin (0) ({figs 1–11}); in basal third or basal half, sheen and punctuation of sutural margin extend onto first or second interstriae (1) (Figures 1A,E, 4); {figs 13–15}).
- 28. Epipleura, shape: entirely horizontal and narrow or curved only at base (0); strongly curved and wide from base of elytron to metacoxa, remainder length horizontal and narrowed (1).

# Abdomen

29. Pygidium, basal margin: complete (0) ({fig. 35}); present, but usually interrupted in the middle by the groove of propygidium (1); absent (2) ({fig. 36}).

# Aedeagus

- 30. Genital capsule, phallobase, ventrobasal margin, shape: entirely (0); with median incision (1) ({figs 53-56}).
- Internal sac, medial sclerite, form: wider and strongly curved (0) ({figs 57–58}); wider and only slightly curved (1) ({figs 59–60}); very fine and strongly curved (2) ({fig. 61}).

# The monophyly of Gromphas

In our analysis, the monophyly of *Gromphas* was strongly supported by eight uncontroverted synapomorphies: outer sides of pterothorax (mesepisternum, metepisternum and sides of metasternum) entirely glabrous (char. 11–1; Figures 1B, 7A), metepisternal tab absent (12-1; Figure 7A), sides of anteromedian angle of metasternum with granulose tegument (13-1); {figs 49–52}), centre of metasternum densely punctate (15-1), inner apical angle of male protibiae with a tiny tubercle (21-1; {fig. 23b}), elytral striae without basal fossae (24-1), epipleura strongly curved and wide from base of elytron to metacoxa (28-1), and ventrobasal margin of phallobase with median incision (30-1; {figs 53–56}). The high support values (bootstrap 99, decay index 7) also give us great confidence in the monophyly of *Gromphas*.

Edmonds (1972) and Philips et al. (2004) stated that the metepisternal tab was absent in Gromphas and Oruscatus; the first author considered the presence the metepisternal tab as one of the defining characteristics of the phanaeines when these two genera are excluded. However, as we observed in Cupello and Vaz-de-Mello (2013), the two species of Oruscatus have, in fact, a short tab in their metepisterna covering the margin of the elytral epipleura, which has an evident depression at this point to receive the tab, in the same way as in Phanaeina (Figure 7B). We observed this same short metepisternal tab and the respective epipleural depression in a series of other dung beetle genera, including species of Copris Geoffroy, 1762, Dichotomius Hope, 1838 (Figure 7D), Chalcocopris Burmeister, 1846, Homocopris Burmeister, 1846, Ontherus Erichson, 1847, Canthidium Erichson, 1847, and Isocopris Pereira & Martínez, 1960, in the tribe Coprini, Helictopleurus d'Orbigny, 1915, Liatongus Reitter, 1893 and Euoniticellus Janssens, 1953, in Oniticellini, and Bubas Mulsant, 1842, in Onitini; in Eucraniini, the putative sister tribe of Phanaeini (Philips et al. 2004; Tarasov and Génier 2015), we have not seen this structure. Nonetheless, the metepisternal tab seen in Phanaeina is unique among the dung beetles by its great development, being much more curved and longer than in any other group observed by us (Figure 7C). Therefore, we consider that this unique form, rather than its mere presence, is one of the defining synapomorphies of Phanaeina. In its turn, Gromphas is exclusive among the Phanaeini in that it has no trace of a metepisternal tab (Figure 7A). The epipleura, however, has a perceptible vestigial depression at the same point as in Oruscatus and the other Phanaeini, indicating again that a metepisternal tab could have been present in the ancestors of the Gromphas. Edmonds (1972, pp. 814–815) hypothesized that the metepisternal tab anchors the elytra, maintaining 'close elytral appression along the elytral suture by restricting lateral slippage of the elytra'. Giving assistance during digging, probably this is the same role that the metepisternal tab has in those other dung beetles, which are fossorial and paracoprid.

The presence of only four protarsomeres, rather than five, is also unique to *Gromphas*, at least among the Phanaeini. In this tribe, protarsi, if present, are found only in females, but 'are always reduced in size and clawless' (Edmonds 1972, p. 770). In some groups, protarsi are completely absent. *Bolbites* and *Oruscatus* are included in this latter case and, in consequence, it is difficult to say if the condition seen in *Gromphas* (i.e. protarsi with four tarsomeres) was the ancestral condition of Gromphadina and then *Oruscatus* took a step further and lost completely the protarsi, or if the condition in the last common ancestor was the five-articulated protarsi and then the reduction occurred in *Oruscatus* and *Gromphas* independently. So, in the first case, protarsi with four tarsomeres would be a synapomorphy of Gromphadina, whereas in the latter case it would be a synapomorphy of Gromphas. Given these difficulties in the ambiguity of this character, we chose not to include it in the analysis.

### The phylogenetic relationship of the species of Gromphas

The six species of *Gromphas* are divided into two main clades, one including *G. aeruginosa* and *G. lemoinei* (clade A in Figure 6), and other including the topology (*G. dichroa* (*G. inermis* (*G. amazonica* + *G. jardim*))) (clade B). The first clade is supported by 10 synapomorphies (four uncontroverted, two controverted by homoplasies, and four ambiguous optimized manually):

genae smooth adjacent to the eyes (char. 4–1; ambiguous and homoplastic with *Oruscatus*; {figs 24, 25}), cephalic projection developed as a horn flattened anteroposteriorly (5-2; ambiguous; {figs 29, 30}), centre of pronotum with a mid-longitudinal line of smooth and glossy tegument (7-1), presence of pronotal prominence (9-1; {figs 1–11}), ventral carina of protibiae simple in both sexes (16-1; {fig. 22}), protibiae with apical tuft of setae without any sexual dimorphism (19-1), protibiae very broad in both sexes (20-1), elytral striae carinulate (25-1; homoplastic with clade D; {fig. 37}), pygidium without basal margin (29-2; ambiguous and homoplastic with clade C; {fig. 36}), and medial sclerite of internal sac wider and strongly curved (30-0; ambiguous; {figs 57, 58}). The values of support are high (bootstrap 99, decay index 6) and give confidence to our hypothesis that these two species are closely related (Cupello and Vaz-de-Mello 2013).

One of the most interesting features of this clade is the reduced sexual dimorphism. In G. aeruginosa and G. lemoinei, the ventral carina of protibiae is simple in both sexes ({fig. 22}), whereas it is ornamented with tubercles or teeth in Oruscatus (Figure 8B), Bolbites (Figure 8C) and in three of the other four Gromphas (G. jardim is the exception) (Figure 8A). In the other Phanaeina, this carina is also simple in both sexes. Other reductions in sexual dimorphism are the protibiae very broad and the protibial tuft of setae of same length in both sexes. In the other Gromphas (and Oruscatus and Bolbites), males have narrower protibiae and the tuft of setae is much longer and denser in males than in females (Figure 2, {fig. 23}). The presence of a pronotal prominence is also a remarkable characteristic of this clade, being absent in the other Gromphadina; nonetheless, as is typical for these two species, there is no sexual difference in this feature. In Phanaeina, in general, males have very elaborate ornamentation on head and pronotum, and it has been known since Darwin (1859, 1871) that these structures play a key role in the sexual access to females by males and, therefore, are under constant pressure from sexual selection (see, for example, Otronen 1988; Rasmussen 1994; Escobar 2003; Emlen and Philips 2006; Rowland and Emlen 2009). But what would be the reason for these structures being as developed in females as in males in this clade? A few other groups of Phanaeini also have females with ornamentation greatly developed, as in males, including those of the group lancifer of subgenus Megaphanaeus d'Olsoufieff, 1924, of Coprophanaeus d'Olsoufieff, 1924, and, to a lesser extent, the group faunus of Sulcophanaeus d'Olsoufieff, 1924, groups that include some of the largest dung beetles of the New World (Edmonds 2000; Edmonds and Zidek 2010). Otronen (1988) supposed that females of Coprophanaeus (M.) ensifer (Germar, 1821) need a developed armature to face combat against other females and so obtain enough food for their large larvae; larvae of smaller dung beetles, on the other hand, do not need large amounts of food and therefore females of these species do not need to face such fierce disputes. Not having such a large size, females of G. aeruginosa and G. lemoinei are unique in possessing well-developed ornamentation. Only with a greater knowledge of their biology will we be able to answer this question more firmly, but it is possible that some idiosyncrasy in their behaviour leads females to fight battles and so be in need of such armament.

The second main lineage within *Gromphas*, clade B, is supported by five synapomorphies (three uncontroverted, two ambiguous): cephalic projection as a carina with base wider than apex (char. 5–1; ambiguous; {figs 31–33}), pronotum globular (10-1), ventral carina of male protibiae with a row of tubercles on basal half (17-2; ambiguous; {fig. 23b}), protibial spur strongly expanded at apex (18-1; {fig. 23}), and, on basal third or basal half, sheen and punctation of sutural margin of elytra extend onto first or second interstriae (27-1; {figs 13–15}). The values of support for this clade, however, are the lowest in our analysis (bootstrap 55, decay index 2). One interesting synapomorphy of this lineage is the form of the ornamentation of the ventral carina of male protibiae. In *Bolbites*, this carina has few tiny, irregular teeth and one large central tooth (Figure 8C); in *Oruscatus*, this ornamentation is modified into a single central tooth without any accessory teeth or tubercles (Figure 8B). In *G. dichroa, G. inermis* and *G. amazonica*, the carina has a row of tiny, regular tubercles, with no apparent difference between these species ({fig. 23b}); in *G. jardim*, as a controverted autapomorphy (char. 16–1, homoplastic with clade A), this ornamentation is lost and the carina is simple and continuous (Figure 2A).

The next clade, clade C, is supported by five synapomorphies (two uncontroverted, three ambiguous): apical margin of clypeus evidently upturned (1-1), lateral margin of clypeus lobate (3-1; Figure 1F), cephalic carina emarginate apically (6-1; ambiguous; Figure 7), pygidium without basal margin (29-1; ambiguous and homoplastic with clade A; {fig. 35}), and medial sclerite of internal sac wider and only slightly curved (31-1; ambiguous) ({figs 59, 60}). The support values give us confidence in this hypothesis (bootstrap 76, decay index 2). This lineage shares with G. aeruginosa and G. lemoinei one important condition, the basal margin of pygidium completely absent ({fig. 36}). Gromphas dichroa, in its turn, possesses the basal margin complete as Bolbites and the other Phanaeina ({fig. 35}). The two species of Oruscatus apparently have an intermediate condition: the basal margin is present, but in the majority of specimens it is interrupted in the middle by the sulcus of propygidium. So, albeit complete in G. dichroa, we believe that there is a general tendency in Gromphadina for the loss of this basal margin, perhaps linked to the great development of the propygidium (which has the length of the pygidium in Gromphadina, and is shorter than the pygidium in Phanaeina), and, therefore, we judge that the most likely scenario was the parallel and independent loss in both lineages rather than a unique loss in the ancestral Gromphas and a new origin in G. dichroa. The form of the medial sclerite of the internal sac of this lineage is very different to that of clade A and G. dichroa and, at same time, homogeneous between its species ({figs 59, 60}). As this sclerite is absent both in Bolbites and Oruscatus, it was not possible to properly polarize this character and, given the topology of the tree, it remained ambiguous in our analysis.

The last clade includes *G. amazonica* and *G. jardim*, sharing four apomorphies (two uncontroverted and two controverted): centre of metasternum with sparse punctation (15-2; homoplastic with *G. aeruginosa*), tubercle of apical inner angle of protibiae modified in a strong spur (22-1; Figure 2, {fig. 21b}), apical protarsomere with spiniform projection at apex (23-1; {fig. 45}), and elytral striae carinulate (25-1; homoplastic with clade *G. aeruginosa* + *G. lemoinei*;{fig. 38}). The support values are also robust (bootstrap 78, decay index 3). The most remarkable synapomorphy of this lineage is the protibial tubercle developed into a strong spur, which has no parallel within the genus; the great differences between the two species regarding the form of this spur are discussed in the description of *G. jardim* above.

## **Phylogenetic conclusion**

Through this phylogenetic analysis, we observed that features related to tegument [e.g. punctation (chars. 17 and 26) or carinulae of elytral striae (char. 25)], which are of a great importance for species identification, were the most error-prone characters for the construction of primary homologies and, so, led to more homoplasies (see Nixon and Carpenter 2012 on homoplasy as error). The differences in pronotal granulation were also very difficult to codify and to include in our analysis because of their gradual variation between species. In fact, there is no pair of species of Gromphas with the same pattern of pronotal granulation. For the same reason, codifying the differences in the form of the anteromedian angle of metasternum was virtually impossible. Nonetheless, in this latter case, there is a clear homogeneity among the forms founded in G. amazonica, G. jardim and G. inermis ({figs 50, 51}), on one side, and in G. aeruginosa and G. lemoinei ({fig. 52}), on the other. The form seen in G. dichroa, which is high, narrow and truncate apically, is unique in the genus ({fig. 49}). Finally, the usual apomorphic absence of posterior pronotal fossae in G. inermis and G. amazonica appeared ambiguous in our analysis, with two possible scenarios: the loss of the fossae in the ancestral of clade C and its subsequent reappearance in G. jardim, or independent losses in G. inermis and G. amazonica. In this case, we have no opinion on which scenario would be more likely and therefore we have not plotted this character on the tree.

We consider that the results of this phylogenetic analysis are important not only because they allows us to reconstruct the evolution of *Gromphas*, but, on a larger scale, because they represent a further contribution to the understanding of the evolution of the dung beetle fauna of the New World. Other American genera with published cladistic analyses of their species are *Ateuchus* Weber, 1801 (Kohlman 1984; only North American species), *Ontherus* Erichson, 1847 (Génier 1996), *Bdelyrus* Harold, 1869 (Cook 1998, 2000), *Cryptocanthon* Balthasar, 1942 (Cook 2002), *Scatimus* Erichson, 1847 and *Scatrichus* Génier and Kohlmann, 2003 (Génier and Kohlmann 2003), *Phanaeus* MacLeay, 1819 (Price 2007, 2009) and *Zonocopris* Arrow, 1932 (Vaz-de-Mello 2007).

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